

RESEARCH ARTICLE

Sexual and reproductive traits of the pearl oyster shrimp *Pontonia margarita* (Decapoda: Palemonidae), symbiotically inhabiting the mantle cavity of the rugose pen shell *Pinna rugosa* (Bivalvia: Pinnidae)

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ABSTRACT. Symbiosis between decapods and mollusks provides a unique opportunity to examine some of the evolutionary strategies employed by marine invertebrates. We describe the sexual and reproductive traits of the pearl oyster shrimp, *Pontonia margarita* Verrill, 1869, found symbiotically inhabiting the mantle cavity of the rugose pen shell, *Pinna rugosa* Sowerby, 1835. Solitary males and females (ovigerous and non-ovigerous) and heterosexual pairs (with ovigerous and non-ovigerous females) were found in a total of 47 rugose pen shells collected from a sandy area with seagrass meadows on the southeastern coast of the Gulf of California, Mexico. The body length (BL) of female *P. margarita* was correlated with the shell volume of their rugose pen shell host. The sex ratio was female-biased (0.85M:1F). Female *P. margarita* were larger than their male counterparts in terms of BL, cephalothorax length (CL), and the maximum chelae length of the second pereopod (MCL). The CL and MCL were more strongly correlated for males ($r = 0.70$, $p = 0.01$). The number and volume of eggs per ovigerous female varied from 95 to 1,571 and from 5.46 ± 0.48 to $8.85 \pm 0.97 \text{ mm}^3$, respectively. Our results indicate polygamous behavior and social monogamy among *P. margarita*, and a short-term pairing system for their association with *P. rugosa*.

KEY WORDS. Monogamy, promiscuity, reproduction, sex ratio, shrimp-pen shell association.

INTRODUCTION

Examples of biological associations between marine invertebrates as evolutionary strategies include small decapods living in or on other organisms, such as anemones, polychaetes, echinoderms, and bivalves (Nizinski 1989, Itani et al. 2002, Baeza et al. 2013). Such associations may occur when guest organisms seek refuge from predators, explore feeding niches, or use their host as a site for reproduction (Baeza 2010a, Hernández et al. 2012, Salas-Moya et al. 2014). However, the relationship between host and guest is often not clearly defined due to environmental conditions and other factors that hamper direct observation and identification of the specific types of association, which can range from commensalism to parasitism. For example, Kennedy et al. (2001) and Rada and Milat (2009) concluded that the association between *Pontonia pinnophylax* (Otto, 1821) and *Pinna nobilis* Linnaeus, 1758 represents commensalism, while Pacheco

et al. (2014) described a mutualistic relationship between the same shrimp species and the bivalve *P. rudis* Linnaeus, 1758.

Symbiosis has been reported between several species of pontoniids and a wide range of host taxa including corals, jellyfish, sponges, and mollusks (Crales 1984, Morrison et al. 2004, Baeza 2008, Baeza and Díaz-Valdés 2011, Baeza et al. 2015). Bivalve hosts inhabited by small shrimp are one of the most studied models of symbiosis (Baeza 2008, Aucoin and Himmelman 2010, Baeza et al. 2013). The morphological, sexual, and reproductive traits of decapods (Richardson et al. 1997, Baeza 2008) in relation to host size (Baeza et al. 2015) are important indicators used to infer the degree of symbiotic association between two species. The host-use pattern and guest mating system can be determined based on the relationship between shrimp size and bivalve size and volume (Góngora-Gómez et al. 2015), the relationship between host body length and shrimp chela and carapace length (Baeza et al. 2011), and the sex and number of

guest organisms in each mollusk species (Rada and Milat 2009). Some researchers argue that symbiotic crustaceans have gonochoric sexual dimorphism (Baeza et al. 2013); that is, they are born, reproduce, and remain either male or female throughout their life. However, other investigators have shown that some shrimp species develop reproductive strategies in response to social behaviors and environmental conditions, including partial changes in sex (Nakashima 1987), strictly protandry (i.e., first males and then females) (Baeza and Piantoni 2010), and simultaneous protandric hermaphroditism (Baeza 2010b).

Specifically, a variety of reproductive behaviors have been observed among symbiotic pontoniids. Pacheco et al. (2014) observed *Pontonia pinnophylax* in the mantle cavity of *P. rudis*, and Baeza et al. (2011) discovered the shrimp *P. mexicana* Guérin-Méneville, 1855 in the amber pen shell *Pinna carnea* Gmelin, 1797. In these studies, both sexual pairs and solitary individuals were reported. The male-female pairs were exclusively heterosexual, suggesting a monogamous relationship (Baeza et al. 2011); nevertheless, the presence of solitary ovigerous females suggests that males abandon the host to look for more females to fertilize (Pacheco et al. 2014). Recently, Góngora-Gómez et al. (2015) described the association between the pen shell *Atrina tuberculosa* Sowerby, 1835 and *P. margarita* Verrill, 1869 in the southeastern Gulf of California, concluding that both organisms maintain a long-lasting relationship and a mating system based on monogamy. In this study, we describe the sexual and reproductive traits of *P. margarita* found symbiotically inhabiting the mantle cavity of *Pinna rugosa* Sowerby, 1835, reporting new morphological and reproductive indicators to better explain this example of symbiosis as an evolutionary adaptation in the marine environment.

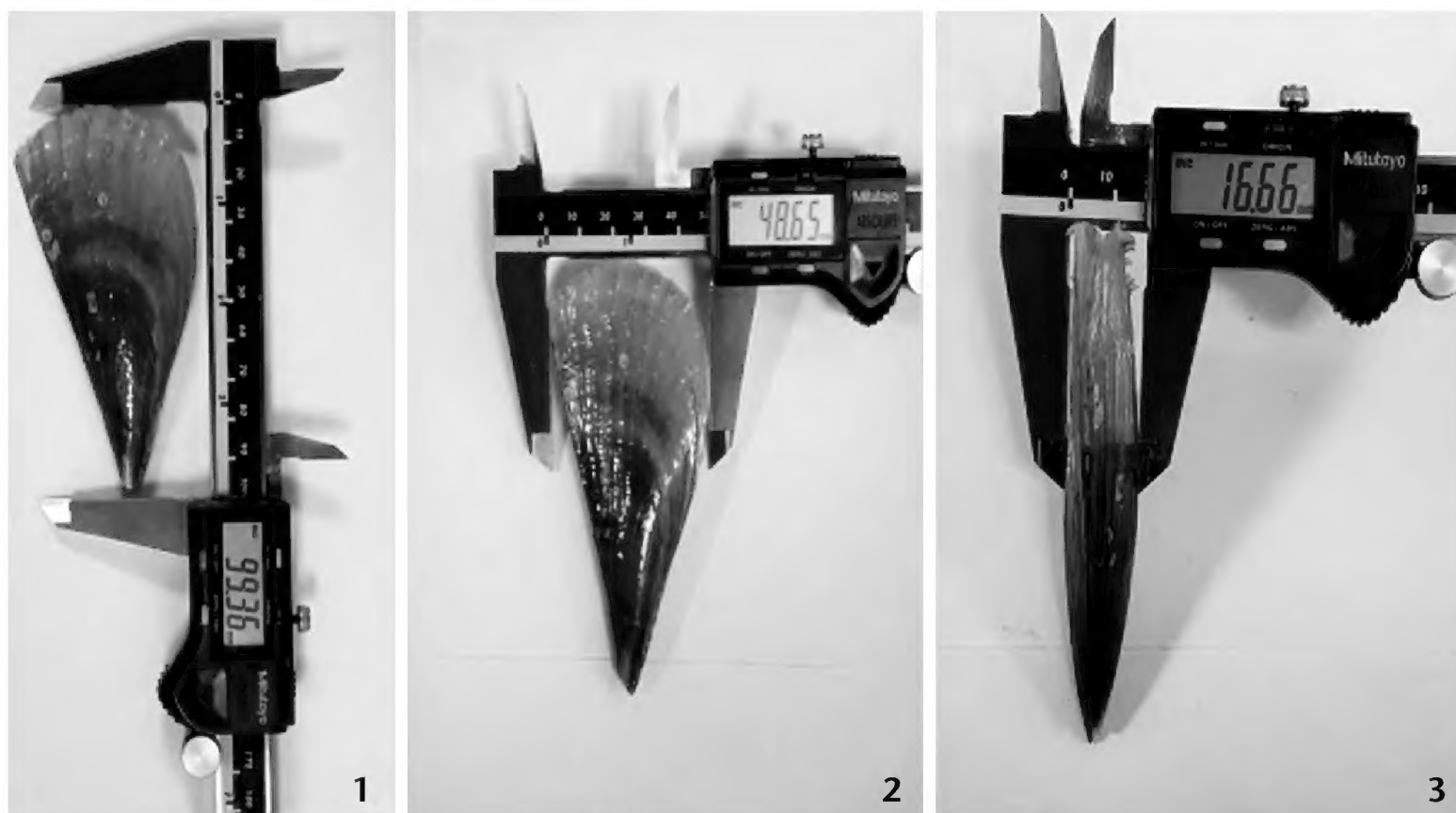
MATERIAL AND METHODS

A total of 47 rugose pen shell (*P. rugosa*) specimens were collected by free-diving during diurnal low tides (< 1 m) in the waters surrounding a fishery in Altata Bay (24°38'00"N; 107°55'00"W), Navolato, Sinaloa, Mexico. The location is a sandy area with *Caulerpa sertularioides* Gmelin, 1768 alga growing in seagrass meadows. Samples were collected between October and December 2017. Once out of the sand but still underwater, each specimen was placed in a separate plastic bag to preserve both host and guest and transported to the Laboratory of Malacology at the Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional at the Instituto Politécnico Nacional (CIIDIR-IPN), Unidad Sinaloa.

Morphometric measurements of the rugose pen shells were obtained using a caliper (± 0.01 mm). The shell height (SH) was measured as the longest point along a line perpendicular from the umbo, the shell length (SL) was the longest point along a line parallel to the umbo, and the shell width (SW) was recorded as the distance from the left to the right side (Figs 1–3).

In order to better understand a possible relationship between the available space of the pen shell for the shrimp (alone or paired, ovigerous or non-ovigerous females), the approximate volume of each rugose pen shell (SV) was calculated multiplying the three morphometric variables according to Salas-Moya et al. (2014) and Góngora-Gómez et al. (2015). The rugose pen shells were sacrificed by cutting the posterior adductor muscle and the mantle cavity was examined for guest organisms.

The shrimp *P. margarita* was identified based on Fransen (2002). The number of guests per host was recorded and all



Figures 1–3. Morphometric measurements of *Pinna rugosa*. (1) Shell height; (2) shell length; (3) shell width.

shrimp specimens were fixed in 70% ethanol. The total body length (BL, from the tip of the rostrum to the tip of the telson), cephalothorax length (CL, from the tip of the rostrum to the posterior end of the carapace), and the maximum chela length of the second pereopod (MCL, from the base of the dactyl and propodus to the tip of the claw) of each shrimp were measured using a caliper (± 0.01 mm) with the aid of a stereomicroscope. The shrimp specimens were stored in the Laboratory of Malacology at the CIIDIR-IPN, Unidad Sinaloa, and coded as: IPN-CIIDIR-SINALOA: Malacología/simbiosis/2017(47).

Several measurements on the reproductive anatomy of each *P. margarita* were recorded (CL and MCL) in order to examine the sexual system. The sex of each specimen was determined based on the position of the genital pore (base of the third and fifth pair of pleopods for females and males, respectively) (Baeza et al. 2013), and the presence or absence of eggs beneath the abdomen was registered. The entire brood mass was detached from ovigerous females ($n = 10$) and distributed in a Petri dish; the total number of eggs was individually counted under microscopic observation. Egg volume, or EV, ($n = 15$ eggs/ovigerous female) was estimated following the formula proposed by Corey and Reid (1991): $EV = (b/2)^2 \times \pi \times a$, where a = major diameter, and b = perpendicular diameter.

The normality and homoscedasticity of data were confirmed using the Lilliefors and Bartlett's tests, respectively (Sokal and Rohlf 1995). Morphometric relationships between rugose pen shell length and total shrimp length, between shrimp measurements (BL, CL, and MCL, by sexes), and between berried female measurements (BL, number of eggs, and EV) were studied using Pearson's correlation (Bhujel 2008). Tukey's test and ANOVA were used to detect possible differences in the EV of ovigerous females. Significant differences in the BL, CL, and MCL by sex were identified using the Student's t-test ($p \leq 0.05$). Data were analyzed using Statgraphics Centurion software for Windows (ver. 14.0).

RESULTS

The rugose pen shell SH varied from 197 to 290 mm and averaged 251.38 ± 22.07 mm. The presence of *P. margarita* in the mantle cavity of rugose pen shells is shown in Table 1.

Table 1. Distribution of *Pontonia margarita* in the mantle cavity of rugose pen shell (*Pinna rugosa*).

Shrimp presence and reproductive condition	Number of observations
No shrimp	15
Ovigerous female + male	6
Non-ovigerous female + male	8
Ovigerous female only	4
Non-ovigerous female only	10
Male only	4

Shrimp specimens were semi-transparent and pale yellow to orange in color (Fig. 4). The pearl oyster shrimp was found in 68% of the total rugose pen shells, inhabiting hosts either in heterosexual pairs ($n = 14$), as solitary females ($n = 14$, Fig. 5), or as solitary males ($n = 4$), with a mean of 0.98 ± 0.01 specimens per rugose pen shell. No rugose pen shells harbored homosexual pairs with two male or two female *P. margarita*. Of the 39 shrimp specimens obtained, 18 were males and 21 females, for a sex ratio of 0.85M:1F.

The smallest rugose pen shell with shrimp had a SH of 198 mm. The BL of female *P. margarita* was the only measure correlated ($r = 0.51$, $p = 0.005$) with the shell volume of *P. rugosa* (1.26 ± 0.26 dm³) (Table 2). There was no correlation between the shrimp body length and host shell height ($r = 0.32$, $p = 0.08$ for females; $r = 0.18$, $p = 0.46$ for males) (Fig. 7).

Table 2. Regression equations, correlation coefficients (r , adjusted for degree of freedom, df), and standard errors of the slopes (SE_s) between *Pontonia margarita* body length (BL) and carapace length (CL) with *Pinna rugosa* shell volume (SV).

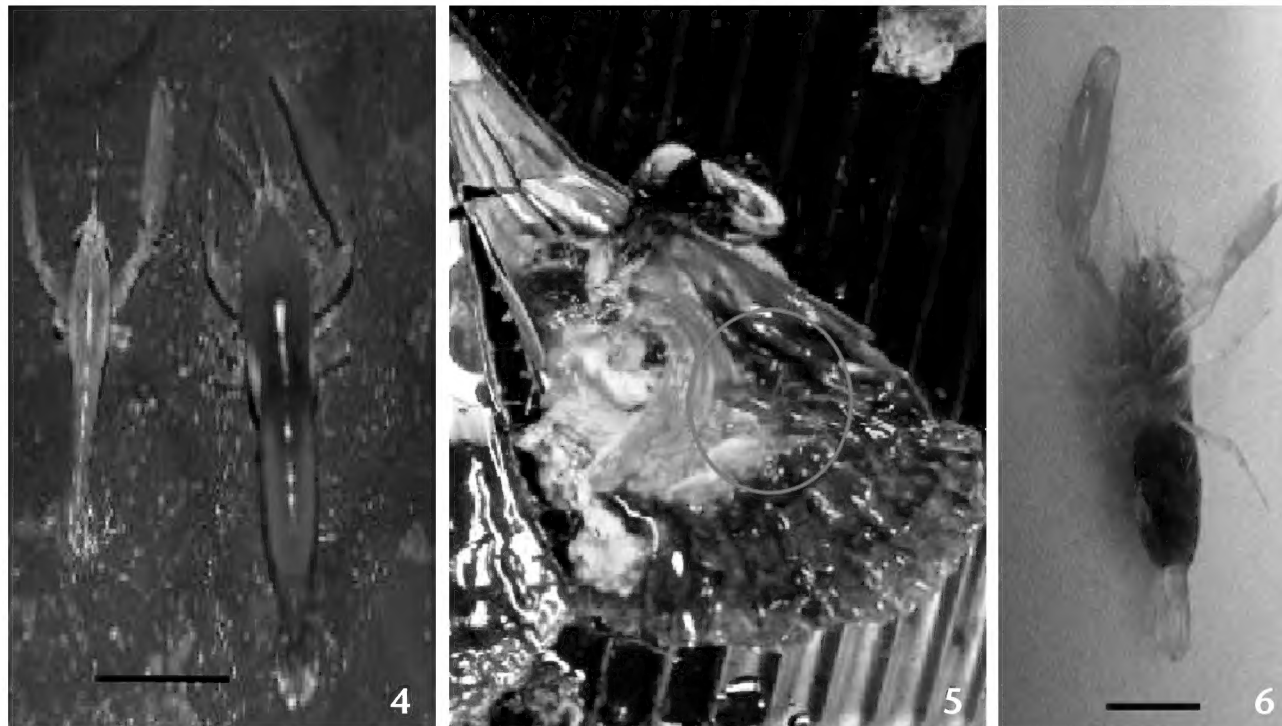
	Regression	R	SE_s	p-value
Females	BL = $-0.399 + 0.052$ SV	0.51	0.27	0.005
	CL = $1.229 + 0.008$ SV	0.11	0.31	0.560
Males	BL = $1.635 - 0.015$ SV	-0.19	0.32	0.444
	CL = $1.409 - 0.021$ SV	-0.22	0.33	0.427

The mean BL and CL of female and male *P. margarita* were 25.15 ± 3.71 and 20.81 ± 7.95 mm, and 9.84 ± 0.16 and 5.05 ± 0.76 mm, respectively. There was no correlation between the BL of males and that of females ($r = 0.19$, $p = 0.49$) in the 14 heterosexual pairs. The BL ($t_{1,14} = 13.03$, $p = 0.001$) and CL ($t_{1,9} = -4.65$, $p = 0.0001$) were significantly longer in female *P. margarita* than in their male counterparts. The CL and MCL were more highly correlated for males ($r = 0.70$, $p = 0.01$). The maximum chelae length of the second pereopod of females (15.61 ± 1.94 mm) was longer ($t_{1,9} = 3.06$, $p = 0.006$) than that of their male counterparts (12.65 ± 3.03 mm).

Of the 21 total females collected, 10 (solitary or paired) were ovigerous. Of the females found with a male in the same rugose pen shell, four were brooding eggs (Fig. 6). The number of eggs per ovigerous female ranged from 95 to 1,571. There was no correlation between the number of eggs and the BL of ovigerous females ($r = 0.52$, $p = 0.12$) or the EV ($r = 0.50$, $p = 0.11$). There were significant differences ($F = 51.31$, $p = 0.0001$) in the EV of different ovigerous females (Table 3). The EV varied from 5.46 ± 0.48 to 8.85 ± 0.97 mm³.

DISCUSSION

Several studies emphasize the importance of the host-guest size relationship between pontoniid shrimps and different bivalve mollusk species. In the present study, shrimps were found



Figures 4–6. *Pontonia margarita*: (4) male (small and whitish) and female (large and orange); (5) female (circled) in the mantle cavity of *P. rugosa*; (6) ovigerous female. Scale bar = 1 cm.

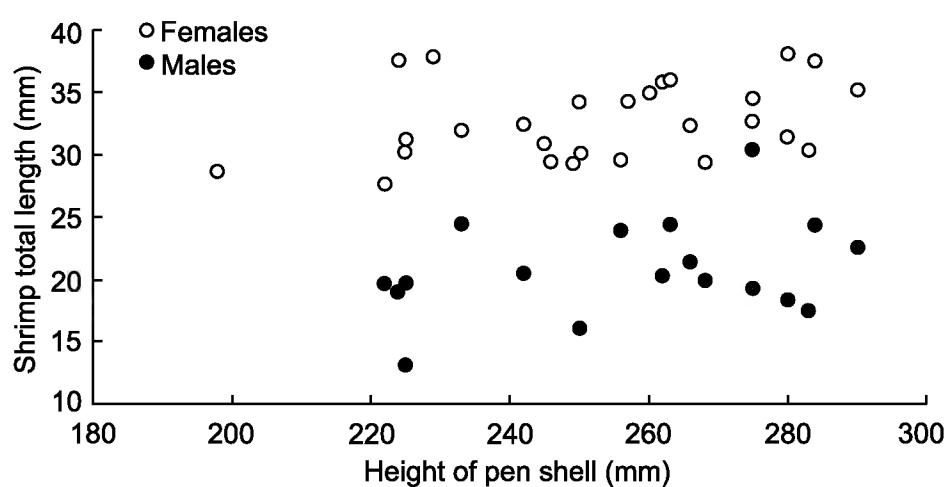


Figure 7. Relationship between *Pontonia margarita* total body length (mm) and *Pinna rugosa* shell height (mm). Regressions for females and males were $r = 0.32$ ($p = 0.08$) and $r = 0.18$ ($p = 0.46$), respectively.

Table 3. Comparison of average egg volume (EV, $n = 15$ eggs per ovigerous female) for ovigerous female *Pontonia margarita* ($n = 10$) in the mantle cavity of *Pinna rugosa*. BL = body length (mm).

BL of ovigerous female (mm)	Mean EV (mm ³)	Standard deviation	Coefficient of variation (%)	Total number of eggs
27.59	8.13 ^{d*}	0.55	6.77	95
29.3	8.68 ^{de}	0.71	8.21	849
31.15	6.16 ^b	0.50	8.15	901
31.94	8.85 ^e	0.97	11.05	1,450
32.59	7.06 ^c	1.08	15.27	104
34.52	9.21 ^c	0.84	9.18	535
34.9	5.51 ^a	0.81	14.81	1,244
35.08	5.46 ^a	0.48	8.89	687
35.8	6.23 ^b	0.46	7.52	1,234
37.54	6.48 ^b	1.49	21.87	1,571

*Significant differences in the mean EV are denoted with different superscript letters ($p < 0.05$).

inhabiting pen shells with an SH varying from 198 to 271 mm, with no correlation between shrimp size and host shell size or any other indication of a size-host preference exhibited by male or female *P. margarita*. Baeza et al. (2013) did not find the shrimp *Paranchistus pycnodontae* Bruce, 1978 in the pearl oyster *Pteria penguin* Röding, 1798 when the bivalve SL was < 175 mm; they concluded that an oyster shell length < 175 mm is too small for the symbiont shrimp. A similar conclusion was reached by Aucoin and Himmelman (2010) when studying the pen shell *P. carnea* as they reported proportional growth between *Pontonia* sp. and its host. The average approximate volume of each rugose pen shell (1.26 ± 0.26 dm³) obtained in this study was smaller than that reported by Góngora-Gómez et al. (2015) for *A. tuberculosa* (3.55 ± 0.76 dm³) using the same morphometric calculations. Our result suggests that the SV of the *P. rugosa* shell is large enough to harbor even a male-female *P. margarita* pair inside, the same shrimp species reported by Góngora-Gómez et al. (2015) inhabiting *A. tuberculosa*. Distinctions between our conclusions and those of the aforementioned studies may be partially explained by the different species of bivalves and mollusks examined. Future studies should report the host volume, SH, and SL as indices of association in order to better evaluate the host-guest relationship.

In this study, shrimps showed an average CL of 9.48 ± 0.16 and 5.05 ± 0.76 mm for females and males, respectively, being similar to the CL average values (females = 8.21 ± 2.46 mm; males 6.39 ± 2.02 mm) reported by Cabrera-Peña and Solano-López (1996) for the same shrimp species inhabiting in the paleal cavity of the pearl oyster *Pinctada mazatlanica* (Hanley, 1856) in Costa Rica, but higher to the mean CL values obtained by Bruce (1980) in *Cainonia medipacifica* (Edmondson, 1935) (reported as *Pontonia medipacifica*) (6.1 and 3.4 mm for females and males, respectively) in the central Pacific (Midway

Island). Differences could partially be explained by shrimp age and host size at sampling.

The lack of a relationship between the BL and CL of *P. margarita* and the SH and SV of *P. rugosa* suggest a short-term pairing for several reasons. First, shrimp specimens were found either alone or in pairs inside the rugose pen shells, suggesting that males and/or females could shift between hosts rather frequently (Baeza et al. 2011). Second, males did not always occur with females in the same host independent of the reproductive condition of the female (measured in this study by the number of eggs and the mean egg volume), suggesting they may abandon females soon after fertilization to look for other females for mating; that is, males display polygamous or promiscuous behavior (Bauer and Abdalla 2001). Similar mating behavior was reported by Baeza et al. (2016) for the shrimp *Pontonia manningi* Fransen, 2000 inhabiting the Atlantic winged oyster *Pteria colymbus* Röding, 1798. Since solitary females were observed brooding eggs in this study, it is possible that males were roaming around different hosts in search of extra-pair copulations (Baeza et al. 2013). However, solitary males were also found in the mantle cavity of *P. rugosa*, an interesting observation that should be explored further. For example, do females also shift from one host to another and do females look for other males for mating?

Third, size-selective pairing, which could favor a proportional size of shrimp pairs inside the host (Góngora-Gómez et al. 2015), has been reported for long-term monogamous free-living symbiotic crustaceans (Mathews 2002, Baeza 2008). However in this study, no correlation ($r = 0.19$, $p = 0.49$) was found between the BL of males and females, indicating that *P. margarita* form pairs for short periods and may move from one host to another.

Fourth, Grafen and Ridley (1983) mention that a male-biased sex ratio favors monogamous behavior as a response to guarding receptive females from other males. However, in our study, more females were found (0.85M:1F), which could favor males moving between host individuals to mate with other females (Baeza and Thiel 2000, Thiel et al. 2003). That is, the presence of more females could promote promiscuous behavior in males instead of social monogamy, when most males occasionally leave a female partner (Baeza 2008), but rarely do males occur alone in the host, as we observed.

Fifth, although the BL of males was smaller, reflecting reverse sexual dimorphism, the maximum chelae length of the second pereopod was proportionally longer than the relationship BL-maximum chelae length in females, which is not only a characteristic of mate guarding (Baeza and Thiel 2007, Asakura 2009) but also, a trait for non-monogamous male shrimps that move between hosts in search of receptive females (Rahman et al. 2003). Finally, crustacean mating has been reported to respond to prevailing environmental conditions; that is, mating occurs mainly when the water temperature is higher (Giese and Pearse 1977). On the contrary to the results reported by Góngora-Gómez et al. (2015) in winter 2004 (water temperature = 19.2 °C), the high water temperature (28.7 °C) we recorded at the sample

site in autumn (October to December 2017) may explain the presence of ovigerous female shrimps and the mating observations. In fact, Gasca and Haddock (2004) highlighted that reproduction of crustaceans in the Gulf of California is related with high water temperatures. Thus, future studies examining samples of *P. margarita* collected from farmed pen shells throughout the year will help elucidate its mating system under the influence of all seasonal variables since farmed pen shells are kept for more than one year from juvenile stages to harvest size ca. > 200 mm (Góngora-Gómez et al. 2017), in captivity.

It is well documented in crustaceans that brood size increases with female BL (Hines 1992, Lardies and Castilla 2001, Salas-Moya et al. 2014). However in this study, no correlation was found between the number of eggs or the EV and BL of ovigerous female shrimps ($r = 0.52$, $p = 0.118$ and $r = 0.50$, $p = 0.109$, respectively). For berried females > 319.4 mm, the number of eggs per female ranged from 687 to 1,450, suggesting brood loss. Also, the egg development stage should be considered to explain the BL of ovigerous female shrimps and the number and volume of eggs. Li et al. (2011) concluded that possible reasons for brood loss of sand shrimp *Crangon uritai* Hayashi & Kim, 1999, include the increasing egg size, which results in reduced area for eggs to attach. Commonly, brood loss is low because females of symbiotic decapods remain in the host during embryo development (Lardies and Castilla 2001). The hypothesis that a reduction in food available to females may force them to consume their own eggs should be evaluated by future research. In our study, the apparent short-term monogamous relationship that implies the displacement of male and female shrimps outside of their host could explain the brood loss we observed. Egg volume is an index of energy content transferred from the female (McEdward and Coulter 1987). The EV obtained for *P. margarita* showed a wide range (5.15 to 8.85 mm³); however, no comparisons with the EV of other pontoniid shrimps are possible due to lack of studies on fecundity.

This is the first report of the symbiosis between *Pontonia margarita* and *Pinna rugosa*. Our study provides new information on the sexual and reproductive traits of *P. margarita* inhabiting the mantle cavity of *P. rugosa* and how this symbiosis shapes the mating system and social behavior of both species. Also important is the inference about the apparent short-term monogamous relationship of this shrimp species inhabiting bivalves as shelters.

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LITERATURE CITED

- Asakura A (2009) The evolution of mating systems in decapods crustacean. In: Martin JW, Crandall KA, Felder EL (Eds) Decapod crustacean phylogenetics. Boca Raton, CRC, 121–180.
- Aucoin S, Himmelman JH (2010) A first report on the shrimp *Pontonia* sp. and other potential symbionts in the mantle cavity of the penshell *Pinna carnea* in the Dominican Republic. *Symbiosis* 50: 135–141. <https://doi.org/10.1007/s13199-010-0050-x>
- Baeza JA (2008) Social monogamy in the shrimp *Pontonia marginata*, a symbiont of *Pinctada mazatlanica*, off the Pacific coast of Panama. *Marine Biology* 153: 387–395. <https://doi.org/10.1007/s00227-007-0815-9>
- Baeza JA (2010a) The symbiotic lifestyle and its evolutionary consequences: social monogamy and sex allocation in the hermaphroditic shrimp *Lysmata pedersenii*. *Naturwissenschaften* 97: 729–741. <https://doi.org/10.1007/s00114-010-0689-4>
- Baeza JA (2010b) Sexual system and natural history observations on semi-terrestrial shrimp *Merguia rhizophorae*. *Invertebrate Biology* 129: 266–276. <https://doi.org/10.1111/j.1744-7410.2010.00200.x>
- Baeza JA, Díaz-Valdés M (2011) The symbiotic shrimp *Ascidonia flavomaculata* lives solitary in the tunicate *Ascidia mentula*; implications for its mating system. *Invertebrate Biology* 130: 351–361. <https://doi.org/10.1111/j.1744-7410.2011.00244.x>
- Baeza JA, Piantoni C (2010) Sexual system, sex ratio and group living in the shrimp *Thor amboinensis* (De Man): relevance to resource-monopolization and sex allocation theories. *The Biology Bulletin* 219: 151–165.
- Baeza, JA, Thiel M (2000) Host use pattern and life history of *Liopetrolisthes mitra*, a crab associate of the black sea urchin *Tetrapygus niger*. *Journal of the Marine Biological Association of the United Kingdom* 80: 639–645.
- Baeza JA, Thiel M (2007) The mating system of symbiotic crustaceans: A conceptual model based on optimality and ecological constraints. In: Duffy JE, Thiel M (Eds) *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford, Oxford University Press, 245–255.
- Baeza JA, Bolaños JA, Hernández JE, Lira C, López R (2011) Monogamy do not last long in *Pontonia mexicana*, a symbiotic shrimp of the Amber pen-shell *Pinna carnea* from the southeastern Caribbean Sea. *Journal of Experimental Marine Ecology* 407: 41–47. <https://doi.org/10.1016/j.jembe.2011.07.011>
- Baeza JA, Hemphill CA, Ritson-Williams R (2015) The sexual and mating system of the shrimp *Odontonia katoi* (Palaemonidae, Pontoniinae), a symbiotic guest of the ascidian *Polycarpa aurata* in the Coral Triangle. *Plos One* 10(13): e0121120. <https://doi.org/10.1371/journal.pone.0121120>
- Baeza JA, Ritson-Williams R, Fuentes MS (2013) Sexual and mating system in the caridean shrimp symbiotic in the winged pearl oyster in the Coral Triangle. *Journal of Zoology* 289: 172–181. <https://doi.org/10.1111/j.1469.7998.2012.00974.x>
- Baeza JA, Simpson L, Ambrosio LJ, Guéron R, Mora N (2016) Monogamy in a hyper-symbiotic shrimp. *Plos One* 11(3): e0149797. <https://doi.org/10.1371/journal.pone.0149797>
- Bauer RT, Abdalla JH (2001) Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda: Caridea): precopulatory mate guarding vs. pure search. *Ethology* 107: 185–199. <https://doi.org/10.1046/j.1439-310.2001.00636.x>
- Bhujel RC (2008) *Statistics for aquaculture*. Ames, Wiley-Blackwell, 222 pp.
- Bruce AJ (1980) Notes on some Indo-Pacific Pontoniinae, XXXV. Further information on *Pontonia medipacifica* Edmonson, 1935. *Crustaceana* 39: 225–235. <https://doi.org/10.1163/156854080X00689>
- Cabrera-Peña J, Solano-López Y (1996) Tamaños y frecuencia de *Pontonia mazatlanica* (Crustacea: Palaemonidae) asociada a *Pinctada mazatlanica* (Bivalvia: Pteriidae), Costa Rica. *Revista de Biología Tropical* 44(2): 915–917.
- Corey S, Reid DM (1991) Comparative fecundity of decapod crustaceans: The fecundity of thirty-three species of nine families of caridean shrimp. *Crustaceana* 60: 270–294. <https://doi.org/10.1163/156854091X00056>
- Criales MM (1984) Shrimp associated with coelenterates, echinoderms, and mollusks in Santa Marta region, Columbia. *Journal of Crustacean Biology* 4: 307–317. <https://doi.org/10.2307/1548028>
- Fransen CHJM (2002) Taxonomy, phylogeny, historical biogeography, and historical ecology of the genus *Pontonia* Latreille (Crustacea: Decapoda: Caridea: Palaemonidae). *Zoologische Verhandelingen Leiden* 336: 1–433.
- Gasca R, Haddock SHD (2004) Associations between gelatinous zooplankton and hyperid amphipods (Crustacea: Peracaridae) in the Gulf of California. *Hydrobiologia* 530(531): 529–531.
- Giese A, Pearse J (1977) General principles. In: Giese AC, Pearse JS (Eds) *Reproduction of marine invertebrates*. New York, Academic Press, 1–49.
- Grafen A, Ridley M (1983) A model of mate guarding. *Journal of Theoretical Biology* 102: 549–567. [https://doi.org/10.1016/0022-5193\(83\)90390-9](https://doi.org/10.1016/0022-5193(83)90390-9)
- Góngora-Gómez AM, García-Ulloa M, Hernández-Sepúlveda JA (2017) Cultivo del callo de hacha (*Atrina maura*) en Sinaloa, México. Colección fotográfica informativa de experiencias en campo y laboratorio. Saarbrücken, Editorial Académica Española, 94 pp.
- Góngora-Gómez AM, Muñoz-Sevilla NP, Hernández-Sepúlveda JA, García-Ulloa II M, García-Ulloa M (2015) Association

- between the pen shell *Atrina tuberculosa* and the shrimp *Pontonia margarita*. *Symbiosis* 66(2): 107–110. <https://doi.org/10.1007/s13199-015-0342-2>
- Hernández JE, Bolaños JA, Palazón JL, Hernández G, Lira C, Baeza JA (2012) The enigmatic life history of the symbiotic crab *Tunicotheres moseri* (Crustacea, Brachyura, Pinnotheridae): Implications for its mating system and population structure. *The Biology Bulletin* 223: 278–290.
- Hines AH (1992) Constraint on reproductive output in brachyuran crabs: Pinnotherids test the rule. *American Zoologist* 35: 503–511. <http://www.jstor.org/stable/3883632>
- Itani G, Kato M, Shiriya Y (2002) Behaviour of the shrimp ectosymbionts, *Peregrinamor ohshimai* (Mollusca: Bivalvia) and *Phyllodurus* sp. (Crustacea: Isopoda) through host ecdyses. *Journal of the Marine Biology Association UK* 82: 69–78. <https://doi.org/10.1017/S0025315402005180>
- Kennedy H, Richardson CA, Duarte CM, Kennedy DP (2001) Diet and association of *Pontonia pinnophylax* occurring in *Pinna nobilis*: insights from stable isotope analysis. *Journal of the Marine Biology Association UK* 81: 177–178. <https://doi.org/10.1017/S0025315401003575>
- Lardies MA, Castilla JC (2001) Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. *Marine Biology* 139: 1125–1133. <https://doi.org/10.1007/s002270100661>
- Li HY, Hong SY, Jin ZH (2011) Fecundity and brood loss of sand shrimp, *Crangon uritai* (Decapoda: Crangonidae). *Journal of Crustacean Biology* 31(1): 34–40. <https://doi.org/10.1651/10-3289.1>
- Mathews LM (2002) Territorial cooperation and social monogamy: factors affecting intersexual interactions in pair-living snapping shrimp. *Animal Behavior* 63: 767–777. <https://doi.org/10.1006/anbe.2001.1976>
- McEdward LR, Coulter LK (1987) Egg volume and energetic content are not correlated among sibling offspring of starfish: implications for life-history theory. *Evolution* 41: 914–917. <https://doi.org/10.2307/2408900>
- Morrison CL, Ríos R, Duffy JE (2004) Phylogenetic evidence for an ancient rapid radiation of Caribbean sponge-dwelling snapping shrimps (*Synalpheus*). *Molecular Phylogenetics and Evolution* 30: 563–558. [https://doi.org/10.1016/S1055-7903\(03\)00252-5](https://doi.org/10.1016/S1055-7903(03)00252-5)
- Nakashima Y (1987) Reproductive strategies in a partially protandrous shrimp, *Athanas kominatoensis* (Decapoda: Alpheidae): sex change as the best or a bad situation for subordinates. *Journal of Ethology* 5: 145–159. <https://doi.org/10.1007/BF02349947>
- Nizinski MS (1989) Ecological distribution, demography, and behavioral observations on *Periclimenes anthophilus*, an atypical symbiotic cleaner shrimp. *Bulletin of Marine Sciences* 45: 174–188.
- Pacheco RJ, Barreiros JP, Goncalves SC (2014) The fan mussel *Pinna rudis* – occurrence and association with *Pontonia pinnophylax* in Terceira Island (Azores, NE Atlantic). *Front Mar Sci. Conference Abstract: IMMR, International Meeting on Marine Research* 2014.
- Rada B, Milat T (2009) The first record of the decapods, *Pontonia pinnophylax*, in *Pinna nobilis* from the southern Adriatic (Croatia) (Decapoda, Natantia). *Crustaceana* 82(11): 1383–1392. <https://doi.org/10.1163/001121609X12475745628469>
- Rahman N, Dunham DW, Govind CK (2003) Social monogamy in the big-clawed snapping shrimp, *Alpheus heterochelis*. *Ethology* 109: 457–473. <https://doi.org/10.1046/j.1439-0310.2003.00885.x>
- Richardson CA, Kennedy H, Duarte CM, Proud SV (1997) The occurrence of *Pontonia pinnophylax* (Decapoda: Natantia: Pontoniinae) in *Pinna nobilis* (Mollusca: Bivalvia: Pinnidae) from the Mediterranean. *Journal of the Marine Biology Association UK* 77: 1227–1230. <https://doi.org/10.1017/S0025315400038741>
- Salas-Moya C, Mena S, Wehrtmann IS (2014) Reproductive traits of the symbiotic pea crab *Austinothere angelicus* (Crustacea, Pinnotheridae) living in *Saccostrea palmula* (Bivalvia, Ostreidae), Pacific coast of Costa Rica. *Zookeys* 457: 239–252. <https://doi.org/10.3897/zookeys.457.7851>
- Sokal R.R, Rohlf FJ (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*. New York, W.H. Freeman and Co., 3rd ed., 887 pp.
- Thiel M, Zander A, Valdivia N, Baeza JA, Rueffler C (2003) Host fidelity of a symbiotic porcellanid crab: the importance of host characteristics. *Journal of Zoology* 261: 353–362. <https://doi.org/10.1017/S0952836903004333>

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